Association of three species of *Strymon* Hübner (Lycaenidae: Theclinae: Eumaeini) with bromeliads in southern Brazil

SIMONE SCHMID^{*1,2}, VOLKER S. SCHMID^{1,2}, RAFAEL KAMKE², JOSEFINA STEINER² AND ANNE ZILLIKENS^{1,2} ¹Med.-Naturwissenschaftliches Forschungszentrum, Universität Tübingen, 72074 Tübingen, Germany ²Department of Cell Biology, Embryology and Genetics (BEG), CCB, Federal University of Santa Catarina, Campus Universitário Trindade, 88.040-900 Florianópolis, SC, Brazil *simigrohme@hotmail.com*

Abstract. As part of a project studying the species richness of bromeliad flower visitors and the diversity and nature of their animal-plant interactions, three species of the lycaenid butterfly genus *Strymon* were recorded as pests of bromeliad inflorescences. *Strymon ziba* fed on the fruits of *Aechmea nudicaulis, S. oreala* on those of *Ae. lindenii* and *Ae. caudata* and *S. serapio* on the dry capsules of *Vriesea friburgensis.* The caterpillars of *S. ziba* and *S. oreala*, pests of cultivated pineapple, were facultatively associated with ants. One *S. ziba* pupa was parasitized by a chalcidid wasp. One *S. oreala* pupa was parasitized by an ichneumonid wasp. Behaviour and life history data of the caterpillars are described and aspects of the host specificity of the lycaenids and potential pest control by parasitoid wasps are discussed.

Key words: *Aechmea*, animal-plant interactions, Atlantic rain forest, Bromeliaceae, Chalcididae, herbivory, Ichneumonidae, parasitism, restinga, *Vriesea*.

INTRODUCTION

Bromeliaceae, a neotropical plant family, can be considered keystone species by providing microcosms for the richness of tropical rain forests due to the high diversity of animal taxa, especially arthropods, associated with them (Frank & Lounibos, 2008). Among the latter, Lepidoptera are major herbivores with many caterpillars feeding upon bromeliad foliage: Napaea eucharilla Bates (Riodinidae) on Werauhia sanguinolenta (Cogniaux & Marchal) J. R. Grant (syn. Vriesea sanguinolenta, Schmidt & Zotz 2000), Aechmea bracteata Grisebach, Ae. nudicaulis (L.) Grisebach (Beutelspacher, 1972) and Ananas comosus (L.) Merrill (Schmidt & Zotz, 2000), Caria domitianus ino Fabricius (1793) (Riodinidae) on *Tillandsia caput-medusae* E. Morren (Beutelspacher, 1972; Frank & Lounibos, 2008), Dynastor darius darius Stichel and D. macrosiris Westwood (Nymphalidae, Urich & Emmel, 1991a, b) on Ae. nudicaulis and Castnia boisduvalii Walker (Castniidae, Biezanko, 1961; Frank & Lounibos, 2008) on T. aeranthos (Loiseleur) L. B. Smith. Beutelspacher (1972) also mentioned Thecla hesperitis Butler & Druce 1872 (Lycaenidae), which is a mistaken record of Ziegleria hesperitis, feeding on Tillandsia caput-medusae, but voucher specimens of "Thecla hesperitis" in UNAM

*Corresponding author

Received: 25 September 2009 Accepted: 15 October 2009 (Universidad Nacional Autónoma de Mexico) examined by Robert K. Robbins are in fact S. serapio Godman & Salvin (1887) (R. K. Robbins, pers. comm.). Not only the plants' vegetative parts, but also their inflorescences contribute significantly to the local faunal biodiversity by providing resources for a great variety of flower visitors that act as pollinators or pollen and nectar robbers (Sazima & Sazima, 1999; Machado & Semir, 2006; Canela & Sazima, 2003; Schmid et al., b, submitted). In addition to causing leaf damage, some herbivorous arthropods associated with bromeliad inflorescences directly interfere with plant reproduction by feeding on reproductive tissues of flowers and fruits, like beetles, butterflies and moths, grasshoppers and even crabs (Fischer et al., 1997; Canela & Sazima, 2003; Frank & Lounibos, 2008). An example of inconspicuous herbivory affecting plant reproductive success was observed in the bromeliads Vriesea friburgensis Mez and Werauhia gladioliflora (H. Wendland) J. R. Grant whose buds are parasitized by Eurytoma wasps (Hymenoptera, Eurytomidae) so no fruits are formed (Gates & Cascante-Marín, 2004; Grohme et al., 2007). Beyond that, cases of seed predation by Cholus and Metamasius weevils (Coleoptera, Curculionidae) (Frank 1999) and Epimorius testaceellus Ragonot 1887 (Pyralidae) larvae that develop in flower pods of Tillandsia fasciculata Swartz (1788) (Bugbee, 1975; Heppner, 1992) have been reported. New World hairstreaks (genus Strymon, Lycaenidae: Theclinae: Eumaeini) use ornamental bromeliads (genera Aechmea, Tillandsia) and the commercial pineapple (Ananas comosus) as host plants

(Robbins & Nicolay, 2002). Strymon megarus Godart 1824 (syn. Thecla basilides, also misspelled as T. basalides) larvae feed on Ananas and other bromeliads like Ae. bracteata (Beutelspacher, 1972; Frank & Lounibos, 2008) and can be considered pest species. Strymon ziba, S. serapio (Robbins & Nicolay, 2002) and S. oreala (Zikán, 1956), the species examined in our study, were reported to eat bromeliads, S. ziba Hewitson 1868 and S. oreala Hewitson 1868 are known pests of A. comosus (Harris, 1927; Zikán, 1956). Since caterpillars and other immature stages of the Eumaeini are small and cryptically coloured, food plants have been recorded for only 25% of the species (Duarte et al., 2005).

Studying the species richness of bromeliad flower visitors and the diversity and nature of their animal-plant interactions in the Atlantic rain forest of southern Brazil, we found lycaenid caterpillars attacking developing fruits. In order to assess the specificity of these associations we examined inflorescences of four common sympatric bromeliad species, *Aechmea nudicaulis, Ae. lindenii* (E. Morren) Baker, *Ae. caudata* Lindman 1891 (Bromelioideae) and *Vriesea friburgensis* (Tillandsioideae), for the presence of larvae and reared them for identification. We also recorded basic data on development, behaviour and natural enemies of the caterpillars.

MATERIALS AND METHODS

Bromeliads with inflorescences were searched for eggs and larvae between November 2006 and June 2008 at four study sites (frost-free subtropical habitats): Santo Antônio de Lisboa and the Environmental Conservation Unit Desterro UCAD (both secondary forest; 27°30'26" S, 48°30'28" W; 27°31'50" S, 48°30'50" W) (Zillikens et al., 2001; Zillikens & Steiner, 2004) as well as Joaquina Beach and Campeche Beach (dune vegetation, Sampaio et al., 2002; 27°40'38" S, 48°28'48" W; 27°37'37" S, 48°26'59" W), on Santa Catarina Island, southern Brazil. All bromeliads examined were growing terrestrially although Aechmea nudicaulis also occurs on trees. In total, 20 infested bromeliads of four species (Aechmea nudicaulis, n = 11; Ae. lindenii, n = 2; Ae. caudata, n = 5; and Vriesea friburgensis, n = 2), growing terrestrially on rocks, in sand or shallow soil, were taken to the laboratory. Presence, size and colour of eggs and caterpillars on the inflorescences were observed regularly every 1-2 days. Ants associated with lycaenid larvae were also collected. When larvae had finished feeding and retreated for pupation, the bromeliad plants were enclosed with fine gauze to capture the emerging adult butterflies.

Voucher specimens of the recorded butterfly, ant and parasitoid species were deposited in the entomological collection of J. Steiner at the Native Bee Laboratory (LANUFSC), BEG, Federal University of Santa Catarina, Florianópolis, Santa Catarina, Brazil.

RESULTS

Three lycaenid species of the genus *Strymon* were reared from the caterpillars found on four bromeliad species. All constitute new records of parasite/ host association. Up to four caterpillars were found simultaneously on one inflorescence.

Strymon ziba (Hewitson 1868)

We found 24 larvae of *S. ziba* on 11 inflorescences of the bromeliad *Aechmea nudicaulis*, yielding an average of 2.2 caterpillars per inflorescence (range 1-4) from November 2006 to January 2007. Seventeen adults emerged in the laboratory, overall sex ratio was 0.7 (M/F). On all inflorescences we detected small white spherical bodies, the eggs from which the larvae had hatched (Fig. 1A, B).

The colour of the larvae was cryptic and changed during their growth from whitish-yellow to reddishpink (Fig. 1C, D). The former matched well to the fruits whereas the latter matched well to the inflorescence stem. The larvae appeared shortly after the end of the flowering period and stayed close to the ripening fruits. Larval feeding behaviour consisted of gnawing a hole into the fruit base large enough for the smaller larval stages to enter the fruit completely and for the larger stages to insert the head and anterior part into the cavity. Through this hole they fed on the soft nutritive tissues of the ovary and ovules, leaving the rigid cortical outer wall of the developing fruit mostly intact (Fig. 1A, B). On an inflorescence of Ae. nudicaulis with two larvae feeding, 30 fruits were damaged, resulting in a mean of 15 fruits damaged per larva. Mean fruit loss per inflorescence was 84.5% (n = 2). Occasionally, the larvae drew back from the fruits to hide under the bracts for about half a day, probably for moulting.

Development in the egg took five days (n = 2). The larval phase lasted 13-15 days (n = 1). The fully grown larvae (≈ 12 -15 mm length) moved into the bromeliad rosette where they pupated on the upper side of the leaves half way between tip and base; one male pupated on a bract of the inflorescence. Pupation took 8-11 days (n = 3). Imagines (Fig. 1E) emerged between mid November until end of January, synchronized to the flowering/fruiting period of *Ae. nudicaulis.*

In the laboratory, caterpillars were occasionally



Figure 1. Strymon larvae on bromeliads on Santa Catarina Island, Southern Brazil.

A-P: Strymon larvae and imagines and associated ants

A-B: Infested fruits of Aechmea nudicaulis, Santa Catarina Island, Brazil. A: Fruit with feeding hole and larval faeces of Strymon caterpillar and a hatched egg of Strymon ziba at the base of the fruit. B: Fruit with feeding hole and a closed egg. C-D: Colour change in Strymon ziba larvae. C: Small, whitish-yellow. D: Larger larva after colour change to reddish-pink. E: Strymon ziba female, collected on Aechmea nudicaulis, Santa Catarina Island, Brazil. Right-hand side ventral view, left-hand side dorsal view. F-I: Ants associated with Strymon ziba caterpillars. F: Crematogaster limata. G: Linepithema iniquum. H: Monomorium sp. (floricola). I: Paratrechina sp. J: Strymon oreala, female, right-hand side ventral view, left-hand side dorsal view. K: Strymon oreala larva feeding on fruits of Aechmea caudata. L: Larva of S. oreala feeding on withered flower petals. M: Tapinoma melanocephalum ant on the back of a S. oreala larva (white arrow). N: Strymon serapio, female, right-hand side ventral view, left-hand side dorsal view. O: Larva of S. serapio on dry fruit of Vriesea friburgensis with feeding hole. P: Dry fruit of Vriesea friburgensis with exuvia of S. serapio inside. Length of exuvia: ≈ 12 mm.

Q-W: Strymon larvae at A. lindenii and parasitoids.

Q-R: Strymon larvae. Q: Strymon larva on A. lindenii feeding on fruit. R: Strymon pupa on infructescence.

S-T: Anisobas, a parasitoid of Strymon sp. S: Lateral view of the Anisobas imago that hatched from the Strymon exuvia. T: Opened Strymon exuvia besides hatched Anisobas imago. U-W: Conura, a parasitoid of Strymon sp. U: Opened pupal case of Strymon sp. V: Imago of Conura sp., dorsal view. W: Lateral view.

tended by ants of four species: *Crematogaster limata* Smith 1858, *Linepithema iniquum* Mayr 1870, *Monomorium floricola* Jerdon 1851 and *Paratrechina* sp. (Fig. 1F-I). Tending worker ants walked over the bodies of the caterpillars and took up small droplets secreted posterodorsally (Fig. 1F).

Additionally, we observed *S. ziba* imagines sucking extrafloral and floral nectar from inflorescences of *Ae. nudicaulis* and one female laying one single egg on each of two recently withered flowers, respectively. The female flew around the inflorescence and sucked nectar of several flowers before ovipositing. The initially greenish eggs turned white after a few minutes. Thereafter, the female left the inflorescence.

Strymon oreala (Hewitson 1868)

We discovered seven larvae of S. oreala (Fig. 1]) on five inflorescences of the bromeliad Ae. caudata (April 2008) and two larvae on two inflorescences of Ae. lindenii (August - September 2007). As described for S. ziba on Ae. nudicaulis larvae fed on the developing fruits of Ae. lindenii and Ae. caudata (Fig. 1K-M) and retreated into the rosette for pupation. Additionally, a larva was seen feeding on withered flower leaves, probably eating old reproductive structures inside the petals (Fig. 1L). On an inflorescence of Ae. caudata with one larva feeding, 15 fruits were damaged. The pupal stage took 15-16 days (n = 4). The larvae were reddish-pink like the inflorescence stem (Fig. 1 K-M). Occasionally, single ants of the species Tapinoma melanocephalum Fabricius 1793 were observed on S. oreala larvae (Fig. 1M).

Strymon serapio (Godman & Salvin 1887)

We detected four brownish-yellow larvae of *S. serapio* (Fig. 1N) on two inflorescences of the bromeliad *Vriesea friburgensis* in secondary forest in December 2007. The larvae chewed a hole into the hard capsule of the developing fruit (Fig. 1O) and fed on the seeds within. Pupation took place inside the empty fruit capsule (Fig. 1P), the imago emerged after 11 days (n = 1).

Parasitoids

On two occasions we found *Strymon* brood infested with a parasitoid. The first case (14 November 2005, Campeche Beach) was a larva on an inflorescence of *Ae. lindenii* (Fig. 1Q). Since the only identified *Strymon* infestation of this bromeliad was by *S. oreala* (see above) we assume that the parasitized larva belonged to the same species. The larva pupated on the infructescence on 18th November 2005 (Fig. 1R). This might, however, not be the usual location for pupating because Aurum® insect glue had been applied to the infructescence stem, thus preventing the caterpillar from moving down to the rosette. After 18 days an ichneumonid wasp of the genus *Anisobas* (subfamily Ichneumoninae) emerged from the pupa (Fig. 1S, T).

In the second case, discovered 6 January 2007 at Santo Antônio, a pupa (Fig. 1U) was located at the upper margin of a leaf of *Ae. nudicaulis* (plant with infructescence). So far, we found this bromeliad species only to be infested with *S. ziba* (see above); hence we assume that the pupa belonged to this species. On 23 January 2007, a chalcidid wasp of the genus *Conura* (subfamily Chalcidinae), "most probably of the *flava* group" (Gérard Delvare, pers. comm.), emerged from the pupa (Fig. 1V, W).

DISCUSSION

Larval behaviour and host plants

Our findings constitute new host records for the associated Strymon species. The only lycaenids so far recorded on Ae. lindenii are larvae of an unidentified species of Thecla on Santa Catarina Island (Lenzi et al. 2006) with a similar feeding behaviour and life history data as described here for S. oreala. It is therefore possible that they did in fact observe larvae of a species of Strymon. Our observations also confirm some life history traits reported by Duarte et al. (2005) such as the cryptic coloration of the larvae which is well adapted to parts of the plants on which they move or feed. Besides the evident association of Strymon larvae with infructescences, they were even more selective in the sense that they fed only on the internal parts of the developing fruits, i.e. the ovaries, but not on leaves, sepals or other plant tissues. By hollowing out the fruits they create their own shelter for feeding or even pupal chambers (in case of S. serapio).

We further report here the first data on the life cycle of the three species, all of which develop within about one month and without diapause. It is therefore likely that the *Strymon* species studied by us are multivoltine having several generations per year. This is in agreement with the pattern reported for other *Strymon* species in the tropics (Opler *et al.* 2009). The choice of hosts by ovipositing females depends on seasonal availability of fruiting plants. The bromeliads studied by us all have relatively short and seasonal fruiting periods, so that only one or two generations can develop on a given plant population.

Adults emerging at the end of a flowering period have to seek for alternative hosts for egg laying. In our study, Strymon oreala was the only species recorded on two hosts both in the genus Aechmea. Interestingly, the inflorescences and flowers of Ae. lindenii and Ae. caudata are very similar in floral morphology and coloration (Kamke, pers. obs.), but Aechmea lindenii flowers from August to November (Dorneles et al., ms) whereas Ae. caudata flowers from March to June without overlap, though single plants of both Aechmea species can be found flowering outside the main flowering period, for example Ae. lindenii on more open areas in restinga sites throughout the year (Lenzi et al. 2006) and Ae. caudata in secondary forest in September (Kamke, pers. obs.). Nevertheless, there is a gap of several months for which we do not yet know the host plants. We know, however, that S. oreala does not attack the infructescences of Ae. nudicaulis or V. friburgensis, which flower between. Therefore, a switch to another host, whether bromeliad or not, must occur in S. oreala, S. serapio and S. ziba.

As *S. ziba* and *S. oreala* are pests of cultivated pineapple it would be interesting to further identify alternative host plant species in order to better understand under which circumstances the larvae reach pest status and to assess their damage to the crop. In this context it is also worth emphasizing our record of a possible natural enemy of *S. ziba*, a parasitoid wasp of the family Chalcididae. Its potential as natural biological control agent should be assessed by elucidating its life history, abundance and host specificity.

Association with ants

As has been reported from other lycaenid caterpillars, the larvae of S. ziba possess a dorsal secretory organ, the Newcomer's gland (Malicky 1970), that might exude honey-like droplets to appease ants. Of the species recorded, Monomorium floricola and Tapinoma melanocephalum are invasive ants (Delabie et al. 1995; Campos-Farinha 2005) and only occurred in the laboratory. We consider the same to be true for Paratrechina sp. for this species was only observed in the laboratory. Crematogaster limata and Linepithema iniquum, however, were frequently found nesting in the bromeliads or visiting their inflorescences (Rosumek et al. 2008, Schmid et al. a, ms) and were thus brought to the laboratory together with the plants taken in the field. These two, at least, may be considered associated with the Strymon caterpillars under natural conditions, albeit only facultatively since larvae observed in the field were mostly not tended by ants.

Diversity of the Strymon - bromeliad association

Our finding that four species of bromeliads were parasitized in very similar ways by *Strymon* larvae is remarkable in yet another aspect. It confirms a relatively high diversity and abundance of sympatric, even syntopic, *Strymon* species in bromeliad-rich Atlantic forest and restinga habitats of southern Brazil. Thus, the fact that three co-occurring species were recorded in studies on only four bromeliad species suggests that a thorough examination of further bromeliad inflorescences might result in the finding of more *Strymon* species and underlines the importance of these plants for sustaining a high diversity of the lepidopteran fauna in the Mata Atlântica.

ACKNOWLEDGEMENTS

We thank Robert K. Robbins for lycaenid identification and valuable help with *Strymon* taxonomy and literature, as well as David Wahl and Gérard Delvare for parasitoid identification. This study is part of the Project "Internal dynamics of rain forest: specificity of animal-plant interaction" within the Brazilian-German program "Mata Atlântica", and we acknowledge the financial support by BMBF (01LB0205A1) and CNPq (590040/2006-5).

LITERATURE CITED

- BEUTELSPACHER, C. R. 1972. Some observations on the Lepidoptera of bromeliads. Journal of the Lepidopterists' Society 26: 133-137.
- BIEZANKO, C. M. 1961. Castniidae, Zygaenidae, Dalceridae, Eucleidae, Megalopygidae, Cossidae et Hepialidae da Zona Missioneira do Rio Grande do Sul. Arquivos de Entomologia Serie B, Escola de Agronomia "Eliseu Maciel" 14 : 1-12.
- BUGBEE, R. E. 1975. A new species of the genus *Eurytoma* (Hymenoptera: Eurytomidae) from a pyralid occurring in the flower pods of *Tillandsia fasciculata*. Journal of the Georgia Entomological Society 10: 91- 93.
- CAMPOS-FARINHA, A. E. 2005. Urban pest ants of Brazil (Hymenoptera: Formicidae). *In:* Proceedings of the Fifth International Conference on Urban Pests. Chow-Yang Lee and William H. Robinson (editors), 81-84.
- CANELA, M. B. F. & M. SAZIMA. 2003. Florivory by the crab Armases angustipes influences hummingbird visits to Aechmea pectinata (Bromeliaceae). Biotropica 35: 289-294.
- DELABIE, J. H. C., I. C. DO NASCIMENTO, P. PACHECO & A. B. CASIMIRO. 1995. Community structure of house-infesting ants (Hymenoptera: Formicidae) in southern Bahia, Brazil. Florida Entomologist 78: 264-270.
- DORNELES, L. L., A. ZILLIKENS, B. HARTER-MARQUES & J. STEINER. SUBMITTED. Mixed pollination by hummingbirds and bees in Aechmea lindenii (Bromeliaceae) in Atlantic Rain Forest at Santa Catarina Island, southern Brazil. Submitted to Entomologia Generalis.
- DUARTE, M., R. K. ROBBINS & O. H. H. MIELKE. 2005. Immature stages of *Calycopis caulonia* (Hewitson, 1877) (Lepidoptera, Lycaenidae, Theclinae, Eumaeini), with notes on rearing detritivorous hairstreaks on artificial dict. Zootaxa 1063: I-31.
- FISCHER, E. A., L. F. L. DUARTE & A. C. ARAUJO. 1997. Consumption of

Bromeliad flowers by the crab *Metasesarma rubripes* in a Brazilian coastal forest. Crustaceana 70: 118-123.

FRANK, J. H. 1999. Bromeliad-eating weevils. Selbyana 20: 40-48.

- FRANK, J. H. & L. P. LOUNIBOS. 2008. Insects and allies associated with bromeliads: a review. Terrestrial Arthropod Reviews 1: 125-153.
- GATES, M. W. & A. CASCANTE-MARÍN. 2004. A new phytophagous species of *Eurytoma* (Hymenoptera: Eurytomidae) attacking *Werauhia gladioliflora* (Bromeliales: Bromeliaceae). Zootaxa 512: 1-10.
- GROHME, S., J. STEINER & A. ZILLIKENS. 2007. Destruction of floral buds in the bromeliad *Vriesea friburgensis* by the phytophagous larvae of the wasp *Eurytoma* sp in southern Brazil (Hymenoptera: Eurytomidae). Entomologia Generalis 30: 167-172.
- HARRIS, W. V. 1927. On a lycaenid butterfly attacking pineapples in Trinidad, B.W.I. Bull. Entomological Research 18: 183-188.
- HEPPNER, J. 1992. Bromeliad pod borer, *Epimorius testaceellus* (Lepidoptera: Pyralidae: Gallerinae). Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Entomology Circular 351: 1-2.
- LENZI, M., J. Z. DE MATOS & A. I. ORTH. 2006. Variação morfológica e reprodutiva de *Aechmea lindenii* (E. Morren) Baker var, lindenii (Bromeliaceae). Acta Botanica Brasilica 20: 487-500.
- MACHADO, C. G. & J. SEMIR. 2006. Fenologia da floração e biologia floral de bromeliáceas ornitófilas de uma área da Mata Atlântica do Sudeste brasileiro. Revista Brasileira de Botânica 29: 163-174.
- MALICKY, H. 1927. New aspects on the association between lycaenid larvae (Lycaenidae) and ants (Formicidae, Hymenoptera). Journal of the Lepidopterists' Society 24: 190-202.
- OPLER, P. A., K. LOTTS & T. NABERHAUS. 2009. Butterflies and moths of North America. Bozeman, MT: Big Sky Institute. Available from: http://www.butterfliesandmoths.org/ (Accessed 23/09/2009).
- ROBBINS, R. K. & S. S. NICOLAY. 2002. An overview of *Strymon* Hübner (Lycaenidae, Theclinae, Eumaeini). Journal of the Lepidopterists' Society 55: 85-100.

ROSUMER, F. B., M. A. ULYSSÉA, B. C. LOPES, J. STEINER & A. ZILLIKENS.

2008. Formigas de solo e de bromélias em uma área de Mata Atlântica, Ilha de Santa Catarina, sul do Brasil: Levantamento de espécies e novos registros. Biotemas 21: 81-89.

- SAMPAIO, M. C., L. E. PERISSÉ, G. A. DE OLIVEIRA & R. I. RIOS. 2002. The contrasting clonal architecture of two bromeliads from sandy coastal plains in Brazil. Flora 197: 443-451.
- SAZIMA, M. & I. SAZIMA. 1999. The perching bird *Coereba flaveola* as a co-pollinator of bromeliad flowers in southeastern Brazil. Canadian Journal of Zoology 77: 47-51.
- SCHMID, V. S., S. SCHMID, J. STEINER & A. ZILLIKENS. a. ACCEPTED. High diversity of ants foraging on extrafloral nectar of bromeliads in the Atlantic rainforest of southern Brazil. Accepted for publication in Studies on Neotropical Fauna and Environment.
- SCHMID, S., V. S. SCHMID, B. HARTER-MARQUES, J. STEINER & A. ZILLIKENS. b. SUBMITTED. Bimodal pollination system of the bromeliad *Aechmea nudicaulis* involving hummingbirds and bees. Submitted to Plant Biology.
- SCHMIDT, G. & G. ZOTZ. 2000. Herbivory in the epiphyte, Vriesea sanguinolenta Cogn. & Marchal (Bromeliaceae). Journal of Tropical Ecology 16: 829-839.
- URICH, F. C. & T. C. EMMEL. 1991a. Life history of neotropical butterflies from Trinidad 4. *Dynastor macrosiris* (Lepidoptera: Nymphalidae: Brassolinae). Tropical Lepidoptera 2: 141-144.
- URICH, F. C. & T. C. EMMEL. 1991b. Life history of neotropical butterflies from Trinidad 5. *Dynastor darius (Lepidoptera:* Nymphalidae: Brassolinae). Tropical Lepidoptera 2: 145-149.
- ZIKÁN, J. F. 1956. Beitrag zur Biologie von 12 Theclinen-Arten. Dusenia 7: 139-148.
- ZILLIKENS, A., J. STEINER & Z. MIHALKÓ. 2001. Nests of Augochlora (A.) esoxin bromeliads, a previously unknown site for sweat bees (Hymenoptera: Halictidae). Studies on Neotropical Fauna and Environment 36: 137-142.
- ZILLIKENS, A. & J. STEINER. 2004. Nest architecture, life cycle and cleptoparasite of the neotropical leaf-cutting bee *Megachile* (*Chrysosarus*) *pseudanthidioides* Moure (Hymenoptera: Megachilidae). Journal of the Kansas Entomological Society 77: 193-202.